

Palaeopathology and injury in the extinct mosasaurs (Lepidosauromorpha, Squamata) and implications for modern reptiles

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Three fossilized dentaries provide an insight into the healing of fractures in a major group of extinct marine predators, mosasaurs. The data has implications for modern day reptiles in which such information is scanty. All three dentaries have callus formation. Both dentaries of *Mosasaurus hoffmanni* show fracture non-union, possibly resulting from intervening tissue. They also show evidence of osteomyelitis. Bone remodeling is complete in an earlier fracture in one of the *M. hoffmanni* dentaries. Given that the most recent fracture (non-union) occurred at a new and much deeper part of the dentary and not in the region of the earlier fracture, it can be assumed that remodeled bone in mosasaurs (probably in reptiles generally) could withstand powerful stresses such as those encountered during predation and fighting. The splenial bone, attached in life to the dentary only by connective tissue, may have acted as a natural splint to immobilize the fracture to the dentary and maintain its alignment during healing. Possible explanations for the injuries are feeding on hard-shelled prey, such as turtles, and fighting. □ Bony callus, dental fractures, disease, fighting, healing, mosasaur.

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Bone pathology described in the present study concerns a prominent group of ancient marine reptile of the latest Cretaceous, the mosasaurs. These were marine varanoid reptiles (see Lee 1997 for an alternative hypothesis on mosasaur ancestry) that perished at the height of their radiation during the major Cretaceous–Palaeogene Mass Extinction 65 Ma (formerly K–T extinction in which the dinosaurs also perished) (Lingham-Soliar 1999). *Mosasaurus hoffmanni* was a giant, reaching lengths of over 17 m, with a head ca. 1.6 m long (Lingham-Soliar 1995). Williston (1897) first drew attention to numerous broken, re-healed postcranial bones of mosasaurs, which he attributed to injuries resulting from a violent lifestyle. Tooth impressions, e.g. on the carapace of a giant sea turtle (Lingham-Soliar 1991) and on ammonite conches (Kaufmann & Kesling 1960), as well as information from gut contents (Dollo 1904; Martin & Bjork 1987), suggest this predatory life-style. However, some authors suggest that the holes on ammonites were made instead by limpets, a view effectively refuted by Tsujita & Westermann (2001; see contra references therein),

Materials and methods

Abbreviations of Repositories. – IRSNB: Institut Royal des Sciences Naturelles d’Belgique, Brussels, Belgium; BMNH: Natural History Museum, London, UK.

Specimens IRSNB R25 and R27 (Figs 1, 2 respectively) belong to *Mosasaurus hoffmanni* and came from the latest Cretaceous Chalk of The Netherlands. Although the material in The Netherlands is occasionally fragmentary, bone surface preservation is invariably excellent. From the size of the preserved dentaries, the estimated skull lengths of IRSNB R25 and R27 are 80 and 60 cm respectively. These are among the smallest specimens of *M. hoffmanni* known and probably represent immature animals (Lingham-Soliar 1995). IRSNB R27 is associated with postcranial material, including a major part of the vertebral column and some ribs and limb bones. None of these show signs of healed fractures or disease. Specimen BMNH R2834 (Fig. 3) belongs to a much smaller species of mosasaur (probably adult), *Platecarpus ictericus*, from the Niobrara Chalk of Kansas, USA.

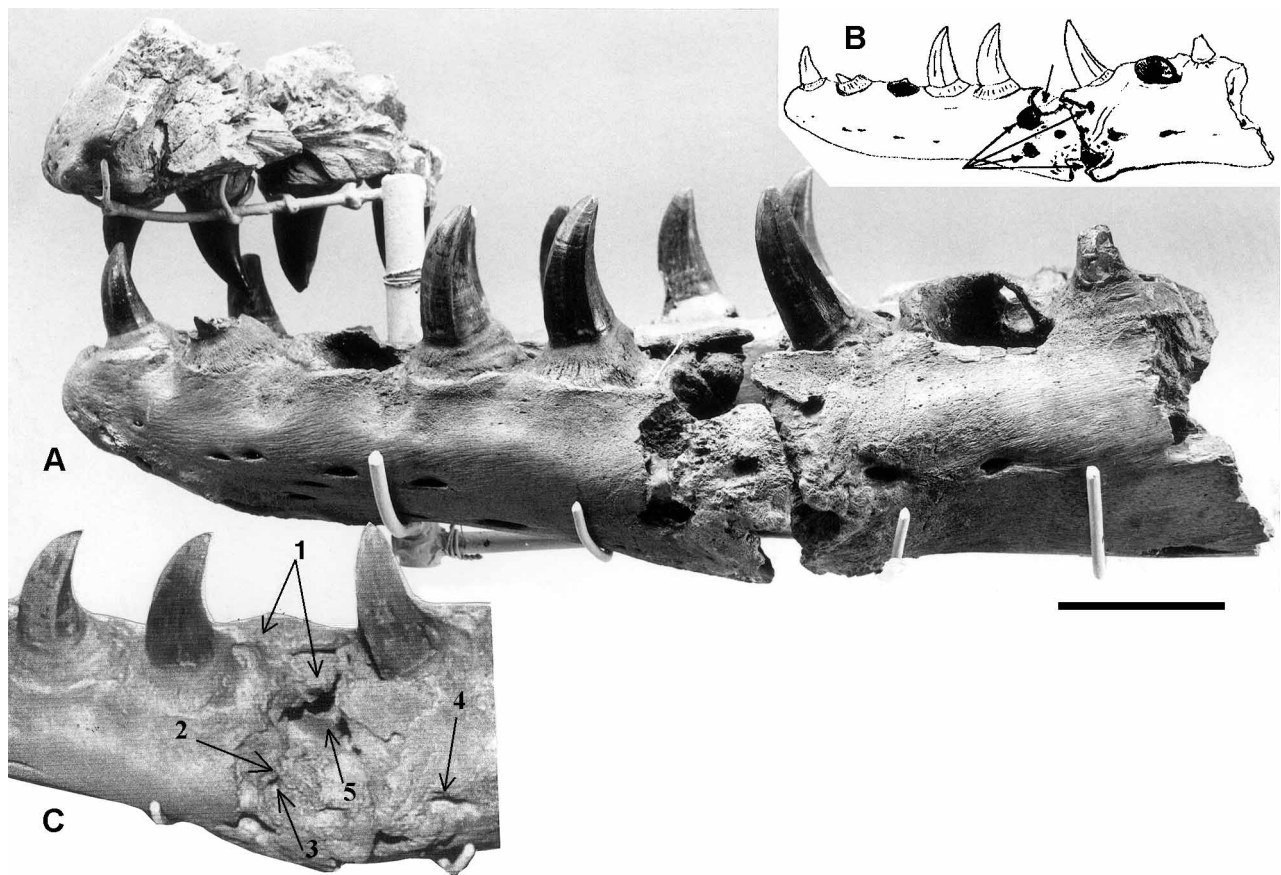


Fig. 1. *Mosasaurus hoffmanni* IRSNB R25, left dentary. □A. Shows the fracture and bony callus associated with infection, in buccal view. □B. (Diagrammatic representation of A) the single arrow shows apparent bacterial erosion around the tooth alveoli. The series of arrows show bacterial erosion on the buccal surface. Two scratches can be seen to the right of the fracture (see text). □C. Buccal-occlusal view showing callus over-growing much of the sixth alveolus (arrow 1), large area of bacterial erosion (arrow 2), osteolytic canal (arrow 3), fifth cranial mandibular canal (arrow 4) and fragment of sixth tooth base (arrow 5). Scale bar (A, C) = 5 cm.

Description and results

A number of observations are made that shed light on the bone-healing processes and lifestyle of mosasaurs. These include: identification of the breaks as a real injury/pathology; state of healing of the bones; strength of re-healed mosasaur fractures; near-perfect alignment of completely fractured dental segments; devitalization and infection of the bony callus. These observations may have implications for modern day reptiles.

Mosasaurus hoffmanni IRSNB R25. – The partial left dentary housed nine teeth, of which four are well preserved (Fig. 1A). Surface preservation is excellent, apart from the area adjacent to the fracture. A complete fracture occurred near the sixth alveolus. The extensive callus is best seen in buccal and sub-occlusal views (Fig. 1A, C). The surface of the bony callus is papulose in appearance and marked by several osteolytic cavities and sinus drainage canals (not to be

confused with foramina for the exits of the fifth cranial nerve, which are not shown by arrows in Fig. 1B). Two parallel scars emerge from this area (Fig. 1A, B). The bony callus has almost completely overgrown the sixth alveolus (Fig. 1C, arrows labelled 1); arrows 2, 3, 4 & 5 show respectively, large area of bacterial erosion, osteolytic cavity, mandibular foramen for cranial nerve V and, fragment of sixth tooth base.

Mosasaurus hoffmanni R27. – The complete right dentary is preserved (the specimen contains other parts of the skull and jaws and post-cranial material). The tips of the anterior teeth are broken-off. Broken teeth on the jaws of *Mosasaurus hoffmanni* are rare and it is possible that these teeth were broken when the dentary was fractured. A well-formed bony callus (Fig. 2A, B) surrounds the fracture non-union (open fracture; see arrow 1). A deep, large pit is present on the lingual surface of the callus (Fig. 2B, C). The pit can be traced as a continuous sinus drainage canal from the internal part of the fracture (seen in the transverse

view of the broken dentary; Fig. 2D). A second smaller pit just below can also be traced from the internal transverse view. On the buccal surface of the dentary there are shallow scratch marks near the bony callus and traces of an associated fracture (Fig. 2A, arrow 2). Apart from a short deep split, where the bone has not knitted (Fig. 2A, arrow 3), a second, virtually healed

fracture can just barely be traced all the way round the dentary. Almost complete re-healing makes it likely that this is an older fracture. In the lingual view of this fracture (Fig. 2C) a slight swelling on the dorsal edge of the dentary (normally straight or slightly concave; arrow) represents the last trace of the bony callus, indicating the greater age of this fracture and that it is

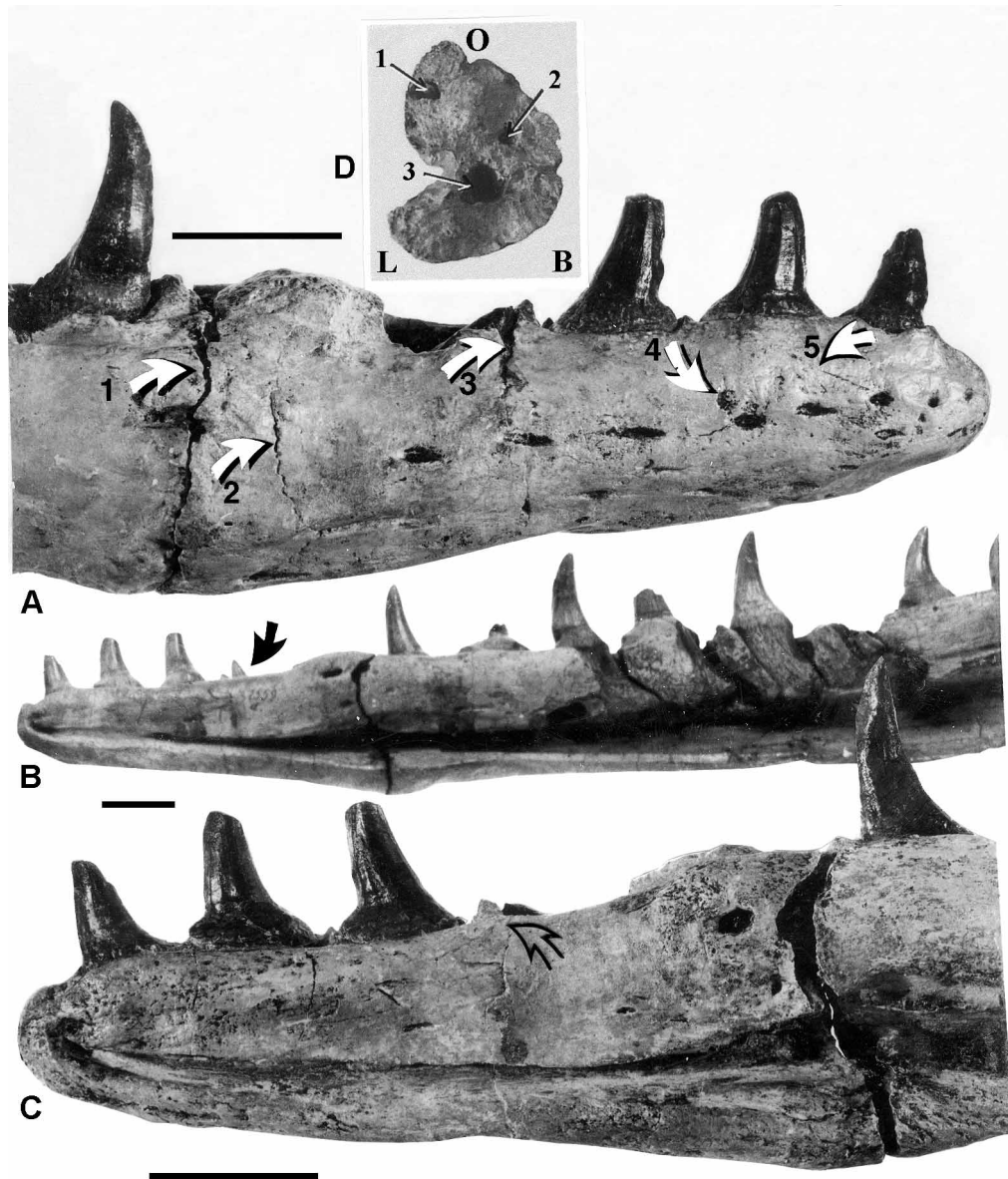


Fig. 2. *Mosasaurus hoffmanni* IRSNB R27, right dentary. □ A. Shows a well-formed bony callus surrounding a fracture non-union (arrow 1) in buccal view. Adjacent to this is an associated stress fracture (arrow 2); toward the middle of the figure is an almost completely healed fracture running round the dentary and completely fused in places (arrow 3). Arrow 4 shows a circular pit anteriorly and arrow 5 a long scratch mark. □ B. Shows best the distinctive bony callus in a wide angled lingual view (arrow shows an emerging replacement tooth). Note the pits near the fracture and the enormous tooth bases. The splenial (see Fig. 3A) is absent. □ C. The detailed lingual view of the dentary shows the abscess pit on the bony callus and the almost completely healed old fracture extending from the fourth tooth base. The arrow points to both the fracture and the slight convex swelling on the upper dental margin that indicates the last trace of the bony callus associated with the fracture. □ D. Transverse section of the anterior part of the broken dentary shows the continuation of the osteolytic pit from the lingual side (arrow 1). A shallow osteolytic pit is also evident (arrow 2). The large pit (arrow 3) represents the canal for cranial nerve V. O = occlusal, L = lingual, B = buccal. Scale bars = 4 cm.



Fig. 3. *Platecarpus* BMNH R2834, right dentary. □ A. Lingual view showing the callus below the second tooth base. Note, the splenial can be seen fitting into the dentary and the posterior mid-jaw articulation is preserved. Anteriorly, the splenial is eroded. □ B. Anterior of dentary in occlusal view showing the swollen bony callus bulging on the lingual surface (curved arrow), which is normally flat and ligamentously bound to the counterpart dentary. Black stippled line shows the missing tip of the dentary, broken-off along the 're-healed' fracture. White stippled line shows the usual flattened shape of the dentary. Small arrow shows traces of the fracture. Scale bar = 5 cm.

not post mortem, taphonomic damage. Anteriorly on the buccal surface there is a circular indentation (Fig. 2A, arrow 4), not to be confused with the mandibular foramina. It apparently represents pre-mortem damage. A thin scar close-by (arrow 5) also suggests pre-mortem damage (below).

Platecarpus ictericus BMNH R2834. – The fracture in this specimen is at the anteriormost tip of the dentary between the first and second dentary teeth (Fig. 3A) and is seen best in buccal view (Fig. 3B). It shows fusion of the fractured segments, with only hairline traces of the fracture visible (Fig. 3B). A distinct bony callus is present (Fig. 3B, curved arrow). This region is normally a flattened sutural contact (Fig. 3B, white dotted line shows extent of callus) with the counterpart dentary. Part of the fractured tip was broken along the fracture and lost during the taphonomic history of the animal (Fig. 3B, black dotted line). The splenial, although eroded anteriorly, is clearly evident and in life was attached to the dentary solely by connective tissue.

Discussion

Identification of a real-life injury in a fossil. – One of the problems of palaeopathology is identification of pre-mortem injuries or disease in fossil animals as distinct from pseudopathologies, artifacts that may resemble pathologies or injury but arise post mortem during the taphonomy of the animal (Bricknell 1987). Identification of the fractures and the condition of the surrounding bone as a pre-mortem injury/pathology is aided in the specimens described here by the

otherwise excellent surface preservation of the dentaries. However, one of the most reliable indications of a pre-mortem fracture in fossilized animals (to distinguish it from a break as a consequence of taphonomic processes) is the presence of a bony callus, seen in all three specimens.

A bony callus may be of further help in determining the age of the injury. Although this is impossible to determine absolutely, one may reliably estimate a minimum and maximum age using current knowledge of bone healing processes. The skull, mandibles (lower jaws) and clavicles or collar bones in reptiles, birds and mammals are membrane bones of dermal origin, the remaining vestiges of dermal plates that protected the body of ancient jawless fishes (ca. 450 million years ago). In birds and mammals within one to two weeks after injury, a provisional bony callus containing secondary fibrocartilage is formed around the ends of the fracture, uniting the fragments and enveloping the fracture site. However, Irwin & Ferguson (1986) demonstrated that fractured reptilian dermal bones, as in amphibians, do not form secondary cartilage. It is clear therefore that the fossilized bony calluses in the present specimens are not provisional cartilaginous precursors probably formed within a few days of the injury (cartilage is rarely preserved in fossils and markedly different from fossilized bone). Endosteal new bone on the other hand forms slowly and may be noted as early as the third week (Irwin & Ferguson 1986; Rothschild & Martin 1993). This gives an estimate of the minimum age of the injury in the present specimens. The bony callus is then resorbed over a period of ca. 16 weeks (Rothschild & Martin 1993), giving an estimate of the upper age of the injury. Thus, the survival after injury of the individuals

described here is probably between ca. 3–16 weeks. This period is noted in parenthesis and is probably a minimum time since bony callus formation and resorption is quite variable and dependent on the animal's general health, e.g. chronic osteomyelitis, poor nutrition etc. could greatly slow the time of bony callus resorption.

Rehealing in the tooth-bearing part of the dentary of an arch predator. – *Mosasaurus hoffmanni* dentaries show fracture non-union despite the presence of distinct calluses. It is, however, possible that the bone broke post mortem along the incompletely healed fracture, as noted above in *Platecarpus* BMNH R2834, although judging from the strength of the earlier fractures in IRSNB R27 this seems unlikely. Fracture non-union has been noted in the postcranial skeletons of a number of animals, e.g. birds, lizards and mammals that have survived in the wild (Harris 1978) and as pseudoarthrosis in the ribs of the extinct ichthyosaurs (reptiles) (personal observation, Staatliches Museum, Stuttgart, Germany).

The nearest comparable injury in mammals is indicated by a bony callus on the posteroventral surface of the mandible of a brown bear. It did not appear to hinder feeding (Dyer 1981), presumably because of the distance from both the teeth and jaw articulations. Harris (1978) figured the skull of a fox with a fracture across the tooth-bearing part of the dentary. The animal was unable to eat and died from starvation before re-healing could occur (indicated by absence of bony callus formation). This kind of fatality in all probability results from inadequate immobilization of the fracture, resulting in failure to feed. Going for extensive periods without food is a much more serious problem in mammals than in reptiles with generally slower metabolic processes.

There is no record in the literature to my knowledge of a re-healed fractured dentary (the toothed portion) in an extant reptile. However, Lambiris (1979) recorded a salamander, *Salamandra* sp. (amphibian), with an ulcerous lesion on the right mandible caused by a fungal infection, the latter resulted in the mandible being broken just behind the mental angle. Dental injury to a lizard, *Agama atricollis* (Dr Angelo Lambiris, University of Durban-Westville (UD-W), personal communication, 2001; Fig. 4, traced from a photograph) shows fracture to the dentary and maxilla that had occurred in the wild. The fracture had united poorly with overlap of the broken ends of the bone. The bony callus had already started to ossify but the animal died from an infection of methicillin-resistant *Staphylococcus aureus*, which resulted from the injury. A further case of injury to a lizard (unpublished; Dr. Angelo Lambiris, personal communication, 2002)

concerns *Varanus niloticus* in which the dentary had been completely fractured in a road accident. A rib splint, used to support the broken halves of the dentary, aided rehealing (Fig. 5) and the animal continued to feed despite the presence of a large callus. Varanoids are particularly relevant in terms of the long held view that they were ancestral to mosasaurs (e.g. De Braga & Carroll 1993) although in recent years snakes have been proposed as more closely related (Lee 1997).

Veterinary records of modern-day reptiles such as crocodiles and large snakes in captivity indicate that they can go for considerable periods without feeding (Dr Angelo Lambiris, personal communication, 2003). Snakes may be able to secrete themselves in burrows, but there are no known observations of such animals in the wild. The problem though is not only one of feeding, especially for larger animals that are unable to hide. For instance, injured crocodiles have to contend with aggression from conspecifics (Meyer 1984). Hence severe dental injuries would clearly be a serious problem for crocodiles in the wild, regardless of whether or not they are able to survive without feeding. Mosasaurs were gigantic animals and some of the problems of injured crocodiles in the wild may be worth considering. It underwrites the need to exercise caution in comparisons with captive animals. For instance, mosasaurs had voracious appetites (e.g. Martin & Bjork 1987) and we have no idea of whether or not they were subject to a blind instinctive feeding behavior (Williston 1897), regardless of whether or not they had the ability to go without food for long periods. This will be considered below.

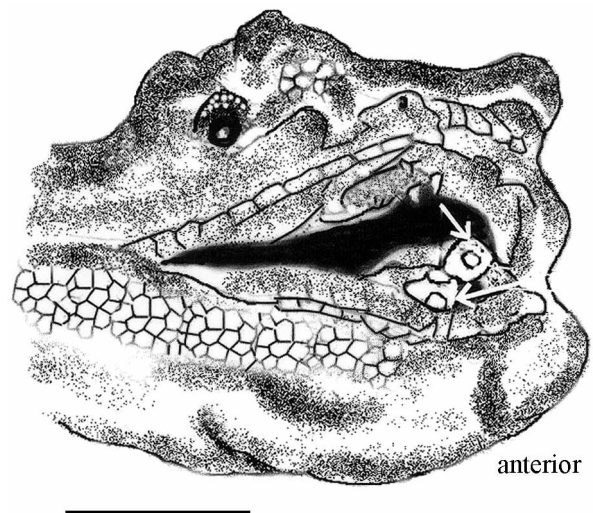


Fig. 4. A drawing from a photograph of *Agama atricollis*. The animal had suffered a broken dentary in the wild and the two parts of the fracture can be seen to have united poorly (see white arrows). Scale bar = 2 cm.

Although the magnitude of the load on a mandible is less than on long bones, the force exerted by food items during feeding will immediately increase the tension that already exists on the occlusal or alveolar surface of the dentary. Hence in circumstances where the dentary is completely fractured, feeding would be almost impossible. For instance, in the treatment of fractured dentaries in animals, effective healing requires a steel plate bolted onto the broken segments or a supportive bone graft (see above). It is clear that immobilization of a fracture is a serious problem for an animal in the wild (see Fig. 4). Such an animal may either change its feeding pattern, by avoiding or restricting feeding or it may instinctively continue aggressive feeding. *Mosasaurus hoffmanni* and the smaller species of mosasaur *Platecarpus* survived severe dental injuries long enough for bony callus formation (and indeed complete healing of earlier fractures), despite the severity of the fractures. Interestingly the alignment of the broken segments of dentary was virtually perfect. Aggressive feeding at this stage would have placed such obvious tension on the occlusal surface of the dentary and distortion of the re-healed bones (e.g. see Fig. 4 of the agama) that it may reasonably be ruled out. This is a strong indication that injured mosasaurs were able to control a vigorous feeding behavior, or ceased feeding for a significant period of time.

Mosasaurs, like snakes, were capable of swallowing prey whole. Hence, some feeding on small prey was potentially possible. Much larger *Mosasaurus hoffmanni* specimens (ca. 17 m long) were described

elsewhere (Lingham-Soliar 1995). Hence, the smaller individuals described here (estimated at 6–8 m long) were in danger from both intra specific and inter-specific aggression (*Hainosaurus bernardi*, a sympatric species was ca. 15 m long (Lingham-Soliar 1992a)), which may well have jeopardized healing of injuries. *Platecarpus*, was probably ca. 4.5 m long and an adult. It would frequently have been among much larger conspecifics e.g. *Tylosaurus*. Consequently, injured animals may have been forced to seek quieter, structurally more complex environments (Lingham-Soliar 1992b, 1999) not frequented by the larger animals.

There are scant records of re-healed skull and dental fractures of reptiles in the wild. Healing in the dentary of *Mosasaurus hoffmanni* (IRSNB R27) may shed light that may be of broader interest to the study of reptiles generally regarding the effectiveness of bone healing. It is clear that the old fracture at the narrow end of the dentary in IRSNB R27 (Fig. 2A, arrow 3, 2C, arrow) had knitted effectively enough to withstand obvious stresses occurring at the time of the latest fracture non-union, given that the latter occurred at a much thicker part of the dentary.

One of the problems sometimes associated with severe fractures is the loss of vascular supply resulting in the devitalized bone becoming necrotic (Rothschild & Martin 1993). However, the condition of the dentaries anterior to the haematomas in specimens IRSNB R25 and R27 is particularly good (note, the presence of one or two alveoli is a normal condition in mosasaurs because of the system of continuous tooth replacement in these reptiles; the tip of a large



Fig. 5. A 1.5 m *Varanus niloticus* specimen that had suffered several injuries to the head, including a fractured right dentary, in a collision with a vehicle. A rib splint supports the fracture (courtesy of Dr Angelo Lambiris, UKZN). Scale bar = 6 cm.

replacement tooth is seen emerging from one). The mandibular artery and fifth mandibular or trigeminal nerve, housed in the mandibular canal (Lingham-Soliar 1998) and extending the length of the dentary, were evidently not damaged. Immobilization of the fracture would probably have helped prevent damage to vital nerves and blood supply to the dentary and will be considered next.

Alignment of fractured dentaries. – An explanation for perfect alignment of the fractured dentaries lies in the peculiar construction of the mosasaur lower jaw. Mosasaur skulls, unlike e.g. those of crocodiles, present-day varanids, and mammals, are kinetic, somewhat resembling the condition in snakes (Lingham-Soliar 1995; Lee *et al.* 1999). The anterior segment of the lower jaw consists of two bones, the dentary and the splenial, which are not fused but ligamentously united. The dentary is a laterally broad girder of bone that houses the teeth. The splenial on the other hand is a laterally flattened flange of bone, deep posteriorly and tapering anteriorly, lying medial to the dentary. The splenial alone forms the articulation with the posterior jaw unit (Fig. 3A). The splenial is missing from the specimens of *M. hoffmanni* described here but in specimens in which it is well preserved it extends anteriorly to approximately the second dentary tooth and overlaps the Meckelian Fossa. This peculiar splenio-dentary association may have played a crucial role in the healing of mosasaur dentaries. During predation the dentary and teeth would take the major part of the force when it closed upon prey. This would only be indirectly transmitted to the splenial via connective tissue, much of it presumably absorbed by the latter and by the mobile splenio-angular joint. It is therefore highly likely that the splenial did not fracture and remained ligamentously bound to the dentary. The intact splenial, bound by connective tissue to the dentary, would have acted as a natural splint that held the fractured segments of the dentary in place. This, together with suppression of aggressive predatory behavior, mentioned above, seems the most parsimonious explanation for the excellent alignment during healing of the jaws.

Bacterial infection. – In specimens IRSNB R25 and R27, pathogenic bacteria may have gained access to deeper tissue from secondary or post-traumatic infections resulting from the fracture and/or from defects in the teeth (caries). Infections affect both hard and soft tissue and are present in fossils as a cavity with a distinct margin (Bricknell 1987; Sawyer & Erickson 1998). In IRSNB R25, the alveolar margin of a missing tooth nearest the fracture (Fig. 1B, arrow) is sig-

nificantly widened and probably represents bacterial erosion that started at the base of the tooth. The papulose surface of the bony callus also suggests considerable bacterial activity. Dental caries may develop as a result of defects in the teeth and the inability to masticate properly etc. (Bricknell 1987). This may be exacerbated by injury, as in the mosasaur specimens described here, or may have contributed to the fracture, as seen in the salamander mentioned above (Lambiris 1979). The smooth margin of the cavity indicates an abscess rather than post mortem damage (Rothschild & Martin 1993; Sawyer & Erickson 1998). Four other cavities (Fig. 1B, radiating arrows) may also represent bacterial erosion, which may continue post mortem for substantial periods of time. Although the buccal surface in IRSNB R27 shows no obvious signs of pustular (pyogenic) cavities and disease, infection is evident on the lingual surface, in the form of a large pit near the dorsal part of the fracture. It represents the outlet of an abscess canal, running from the internal part of the fracture (seen in the transverse view of the broken dentary; Fig. 2D). Because of the excellent surface preservation of this specimen, it adds to the unlikelihood that the cavities and state of the tissue around the fractures resulted from post mortem damage rather than from disease.

Possible causes of the injuries. – Lastly, it is interesting to speculate on the possible cause of the fractures in the specimens. One possibility was mentioned above viz. impact of the jaw against a hard object such as a turtle carapace. The enormous bite-force of *Mosasaurus hoffmanni* (Lingham-Soliar 1991) would clearly have intensified the stress on the dentary. Furthermore, the jaws may have been particularly weakened and vulnerable during tooth replacement, particularly immediately after ejection of the larger teeth (including the massive tooth base) and before the replacement tooth was substantially implanted. A most plausible cause for injuries is attack from other animals. For instance a form of intraspecific competition, snout-grappling, was mentioned by Rothschild & Martin (1993) on the basis of a series of pits on the jaws of a mosasaur specimen. A similar form of intraspecific competition is known in modern-day crocodiles (Meyer 1984). There are signs that this may have occurred in *Mosasaurus hoffmanni*. There are two distinct, finely ulcerated scratches on the bony callus surface of IRSNB R25. The finely pocked surface of the scratches is consistent with the surface elsewhere on the callus but unlike the healthy bone surface elsewhere. This is a good indicator that the scratches were part of the re-healing process and not post mortem damage. The anterior scratch identified in IRSNB R27 is also closely associated with the deep, circular pit,

which resembles a tooth impression (Fig. 2A, arrow 4). Given these characteristics of the older injuries it is highly probable that the animal had suffered earlier aggressive attacks and may support Rothschild & Martin's (1993) conclusions on possible snout-grappling in mosasaurs. The relatively small size of the *M. hoffmanni* specimens described here make it more than circumstantial that these mosasaurs had been victims of intraspecific or interspecific competition involving much larger mosasaurs known at the time in the region. They clearly survived those encounters. Whether or not the most recent injuries led to their deaths cannot be said with certainty, but is a distinct possibility. Restricted feeding may have worked in the short term, but probably not in the long-term survival of the animal, particularly when the healing period is aggravated by infection.

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References

- Bricknell, I. 1987: Palaeopathology of Pleistocene proboscideans in Britain. *Modern Geology* 2, 295–309.
- DeBraga, M. & Carroll, R.L. 1993: The origin of mosasaurs as a model of macroevolutionary patterns and processes. In Hecht, M.K. (ed.): *Evolutionary Biology* 27, 245–322. Plenum Press, New York.
- Dollo, L. 1904: *La vie au sien des mers*. 120 pp. Librairie J-B Baillière et fils, Paris.
- Dyer, D.L. 1981: An analysis of bony changes following trauma to a black bear mandible. *Journal of Wildlife Diseases* 17 (1), 97–100.
- Kaufmann, E.G. & Kesling, R.V. 1960: An Upper Cretaceous ammonite bitten by a mosasaur. *Contributions of the Museum of Paleontology, University of Michigan* 15 (9), 193–248.
- Harris, S. 1978: Injuries to foxes (*Vulpes vulpes*) in suburban London. *Journal of Zoology, London* 186 (4), 567–72.
- Irwin, C.R. & Ferguson, M.W.J. 1986: Fracture repair of reptilian dermal bones: Can reptiles form secondary cartilage. *Journal of Anatomy* 146, 53–64.
- Lambiris, A.J.L. 1979: Surgery on a captive salamander. *British Journal of Herpetology* 5, 843–844.
- Lee, S.Y. 1997: The phylogeny of varanoid lizards and the affinities of snakes. *Philosophical Transactions of the Royal Society, London B* 352, 53–91.
- Lee, S.Y., Bell, G.L., Jr. & Caldwell, M.W. 1999: The origin of snake feeding. *Nature* 400, 655–659.
- Lingham-Soliar, T. 1991: Predation in mosasaurs – a functional approach. In *Natural Structures, Principles, Strategies and Models in Architecture. Sondersforschungsbereich 230* (6), 169–77.
- Lingham-Soliar, T. 1992a: The tylosaurine mosasaurs (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe and Africa. *Bulletin of the Institut Royal des Sciences Naturelle d'Belgique* 62, 171–194.
- Lingham-Soliar, T. 1992b: A new mode of locomotion in mosasaurs: Subaqueous flying in *Plioplatecarpus marshi*. *Journal of Vertebrate Paleontology* 12 (4), 405–421.
- Lingham-Soliar, T. 1995: Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, Upper Maastrichtian of the Netherlands. *Philosophical Transactions of the Royal Society, London B* 347, 155–180.
- Lingham-Soliar, T. 1998: A new mosasaur *Pluridens walkeri* from the Upper Cretaceous, Maastrichtian of the Iullemeden Basin, southwest Niger. *Journal of Vertebrate Paleontology* 18 (4), 709–717.
- Lingham-Soliar, T. 1999: What happened 65 million years ago. *Science Spectra* 17, 20–29.
- Martin, J.E. & Bjork, P.R. 1987: Gastric residues associated with a mosasaur from the Late Cretaceous (Campanian) Pierre Shale in South Dakota. In Martin, J.E. & Ostrander, G.E. (eds): *Papers in Vertebrate Paleontology in honor of Morton Green. Dakoterra* 3, 8–72.
- Meyer, E.R. 1984: Crocodilians as living fossils. In Eldredge, N. & Stanley, S.M. (eds): *Time Fossils*, 105–131. Springer Verlag, New York.
- Rothschild, B.M. & Martin, L.D. 1993: *Paleopathology. Disease in the fossil record*. CRC Press, Boca Raton.
- Sawyer, G.T. & Erickson, B.R. 1984: Injury and diseases in fossil animals. *Bulletin of the Field Museum of Natural History* 58 (6), 20–25.
- Sawyer, G.T. & Erickson, B.R. 1998: Paleopathology of the Paleocene crocodile *Leidosuchus* (= *Borealosuchus*) *formidabilis*. *Paleontology, The Science Museum of Minnesota Monograph* 4, 1–38.
- Tsujita, C.J. & Westermann, G.E.G. 2001: Were limpets or mosasaurs responsible for the perforations in the ammonite *Placentoceras*? *Paleogeography, Paleoclimatology, Paleoecology* 169 (155/3–4), 245–270.
- Williston, S.W. 1897: Range and distribution of the mosasaurs. *Kansas University, Quarto* 6, 177–189.